

ECOLOGY AND MORPHOLOGY OF FEEDING AND AGONISTIC BEHAVIOR IN MUDFLAT STOMATOPODS (SQUILLIDAE)

HUGH DINGLE¹ AND ROY L. CALDWELL²

Chulalongkorn University Marine Biological Station, Ang Sila, Chon Buri, Thailand

Morphological structure co-evolves with the behavior and ecology of organisms. Food habits are influenced by the trophic apparatus, for example, and indeed differences in trophic morphology are often used by ecologists as presumptive evidence of niche differentiation by foraging strategies (*c.g.*, Schoener, 1965, 1974) or of convergent evolution in feeding methods (*c.g.*, Karr and James, 1975). Other behaviors have also co-evolved with morphology; the use of teeth, claws, chelae, etc., in agonistic encounters and displays being cases in point. In this paper data are presented relating morphology to feeding and agonistic behavior in stomatopods, including evidence that, in these animals, differences in sensory capabilities as well as differences in trophic adaptations may be associated with differences in food habits.

Stomatopods are predatory marine crustaceans occurring primarily in a variety of tropical littoral and sublittoral habitats. The chief characteristic of the group is the enlarged second thoracopod (maxilliped) which is used in prey capture and in agonistic interactions. The merus of this appendage is greatly enlarged and extends the length of the carapace or more; the terminal dactylus is also elongate and folds forward under the grooved propodus. The propodus and dactylus can be rapidly unfolded and extended to strike or seize prey or an opponent much like the raptorial prothoracic legs of a praying mantis (hence, the common name of mantis shrimp).

Stomatopods can be divided into two morphological types, the "speakers" and the "smashers", based on the structure of the raptorial appendage and the mode of feeding (Caldwell and Dingle, 1975). In the speakers the dactyl bears teeth and the propodus is usually spined (Fig. 1); these structures are used primarily for seizing and holding prey such as fish, shrimp, snapping shrimp, polychaetes and other relatively soft-bodied organisms, although some evidently take harder items such as thin-shelled pelecypods. The speakers comprise all of three of the four extant families of stomatopod, the Squillidae, Lysiosquillidae, and Bathysquillidae, and part of the fourth family, the Gonodactylidae. The remainder of the Gonodactylidae are smashers. These have a smooth dactyl and propodus (with residual dactylar teeth in some species), and the proximal end of the dactyl is swollen and functions as a hammer (Caldwell and Dingle, 1975). Prey items of smashers include primarily gastropods, pelecypods, crabs, hermit crabs and the like, although other prey can be taken if caught. Prey are captured and then demolished by re-

¹ Present address: Department of Zoology, University of Iowa, Iowa City, Iowa 52242, U. S. A.

² Present address: Department of Zoology, University of California, Berkeley, California 94720, U. S. A.

peated strikes of the raptorial appendage. Spearers occur largely in mud or sand substrates and construct their own burrows, while smashers occur in rock, coral, or rubble and occupy primarily previously existing cavities.

Previous studies (Dingle, 1969; Dingle and Caldwell, 1969; Caldwell and Dingle, 1975, 1977) have demonstrated complex agonistic interactions both within and between species of smashers. In contrast, such behavior in spearers is much less complex, although relative levels of agonism can apparently determine outcomes in interspecific competition (Dingle and Caldwell, 1975). In this paper the relation between behavior, morphology, and habitat in five spearers is analyzed. Three species, *Oratosquilla inornata*, *O. nepa*, and *Cloridopsis scorpio*, are discussed extensively; and some notes on *Harpisquilla harpax* and *O. woodmasoni* are also provided. All these species belong in the family Squillidae (Manning, 1969a, 1971).

MATERIALS AND METHODS

Most animals used in this study were collected from mudflats in the immediate vicinity of Ang Sila, Chon Buri Province, Thailand, situated on the eastern shore of the Gulf of Thailand about 90 km south of Bangkok. Burrows were located at low tide, and the stomatopods were extracted by reaching in one end of a burrow and forcing the occupant out the other (see Dingle and Caldwell, 1975 for details of sampling and a description of the area). Stomatopods were also frequently taken by fishing boats working the waters of the Gulf, and several individuals, especially of *O. nepa*, *O. woodmasoni*, and *H. harpax*, were acquired from fishermen.

In the laboratory the smaller species (30–100 mm), *C. scorpio* and *O. inornata*, were kept in individual containers with a blackened Erlenmeyer flask as a shelter. They were fed every 2–3 days with bits of fish or shrimp, and the water was changed after each feeding. The larger species (70–200 mm), *O. nepa* and *H. harpax*, were kept in large tanks with continuously running sea water and were also fed at 2–3 day intervals. With the exception of two small immature individuals, all specimens of *O. woodmasoni* died before reaching the laboratory.

Observations of agonistic interactions between two individuals were usually conducted between size and sex matched animals in open arenas. These had diameters approximately five times the length of the animals concerned and a sand-covered bottom. These diameters were chosen to maximize contacts between animals for assessing behavioral acts and displays and relative levels of agonism, but still to allow interacting animals to break off and remain apart. Data were voice recorded on tape during the ten minutes of each encounter. Individuals of *O. nepa* from communal tanks were kept isolated for 24 hours before observations were made. A total of 53 ten-minute interactions involving three species were recorded.

In the case of *C. scorpio* and *O. inornata*, observations of burrowing and burrow defense were conducted in large cylindrical glass containers filled to a depth of 15 cm with mud from the natural habitat. Sea water was then added to a depth of 25 cm above the mud. Once the water had cleared, a stomatopod was added and burrowing behavior recorded. Data recording was facilitated by the fact that much of the length of the completed burrow was usually visible, since most animals built against the side of the container. Approximately one day after completion of the

TABLE I

Comparison of body measurements and ratios for five species of squillids.
All values are means except maximum carapace length.

Species	N	Maximum carapace length (mm)	Ratio of cornea width to eyestalk length	Ratio of antennule length to carapace length
<i>H. harpax</i>	5	37.6	1.52	2.12
<i>C. scorpio</i>	11	19.2	.70	1.36
<i>O. inornata</i>	11	18.8	1.33	2.13
<i>O. nepa</i>	11	30.0	.87	1.69
<i>O. woodmasoni</i>	5	25.4*	—**	2.09

* Largest museum specimen (see Methods). Specimens comparable in size to *O. nepa* were taken at Ang Sila.

** See Methods for explanation of absent *O. woodmasoni* measurement.

burrow, a second animal was introduced, and data recording was begun when it perceived the burrow entrance (indicated by an approach toward the entrance with eyes and antennules oriented toward it) and attempted entry. Data were recorded either until an eviction occurred or until five minutes had passed with no attempts by the intruder to gain entry to the burrow. A total of 32 burrow defense interactions were observed.

Morphological measurements were made with calipers on preserved specimens captured at Ang Sila, supplemented by measurements on specimens in the collection of the U. S. National Museum. The data from museum specimens are included only in the plots in Figure 3. Much of the Ang Sila collection was damaged in transit; the data in Table I are taken only from the least damaged Ang Sila specimens with the result that sample sizes are small. Differences between species, however, are still apparent. All specimens of *O. woodmasoni* were seriously damaged, so data perforce are from museum material and only dimensions least affected by preservation are included. Detailed descriptions of the various body measurements are given in Manning (1969b), and his techniques were followed in all cases.

RESULTS

Morphology and prey capture

Based on laboratory observations of prey-capture behavior, *H. harpax* is capable of catching and consuming fish without difficulty, while the other species are not. In parallel experiments eight small (40–70 mm) laterally compressed fish of the same species were introduced into each of two large aquaria: one containing seven *O. nepa* of about 180 mm long, and the other containing seven similarly sized *H. harpax*. Within a few seconds, two of the fish in the *H. harpax* tank had been captured and were being eaten, and by the end of twelve hours all had been consumed; until captured, the fish associated in a tight school. In contrast, no fish in the *O. nepa* tank were captured in the twelve hour observation period, and they did not school.

The behavior of the two species of stomatopods toward the fish was also conspicuously different. *H. harpax* stalked fish or tracked them with eyes and anten-

nules, striking by rapid extension of propodus and dactyl when they were approximately 50–150 mm ahead of or above the stomatopod. If the strike was successful (approximately 30–50% of the time depending on the experience of the fish), the fish was clasped between dactyl and propodus and brought to the mouth where it was also held by the remaining maxillipeds while being chewed upon by the mandibles (see illustrations in Caldwell and Dingle, 1976). *O. ucpa*, on the other hand, struck only when a fish was 20–30 mm in front of the head and usually only when fish actually blundered into the antennules. Two fish were captured and both easily escaped; following the escape, the stomatopod in each case swam around for several seconds sweeping the bottom of the aquarium with laterally oriented back and forth movements of the antennules, evidently seeking the prey on the bottom. On several occasions live fish were put in the home containers of individual *O. inornata* and *Cloridopsis scorpio*. In no case did an individual of either species succeed in capturing one of these fish. In fact, fish and stomatopod often shared a container for several days.

Gut analysis suggested that the diets of *Oratosquilla* spp. and *C. scorpio* consist mostly of crustaceans, annelids, and thin-shelled pelcypods (Dingle and Caldwell, 1975). It was impossible to make a quantitative assessment of dietary overlap between the species because stomatopods completely fragment food before ingestion, but the three species apparently do take qualitatively similar food items. What is also interesting is that these species all evidently take some pelcypods, which although thin shelled, still require smashing before consumption. In this respect, at least, the diets of these spearers are similar to those of smashers (Caldwell and Dingle, 1975, 1976). In contrast to their lack of success with fish, both *C. scorpio* and *O. inornata* readily captured and ate small snapping shrimp (Alpheidae) which were common in the stomatopod habitats. The diet of *C. scorpio* differs from the *Oratosquilla* species in that stomatopod remains were also found in the gut. No gut contents of *H. harpax* were identified, either because of a fish diet or because they had not fed for several hours by the time they were brought to shore by fishing boats.

The most conspicuous difference in trophic apparatus in the species studied was that occurring between the fish-catching *H. harpax* and the others. First, *H. harpax* has a propodus bearing heavy, sharp spines on the anterior margin and a dactyl with eight teeth. In contrast, *Oratosquilla* spp. and *C. scorpio* possess mostly soft, comb-like spines on the anterior margin of the propodus and five (*C. scorpio*) or six (*Oratosquilla*) teeth on the dactyl (Fig. 1). Secondly, the raptorial appendage of *H. harpax* is relatively more elongate with the folded propodus and merus extending beyond the posterior margin of the carapace (Figs. 1 and 2). This length difference is evident in Figure 3, where the "reach" of the raptorial appendage is plotted against carapace length in the five species studied. Reach is defined here as the straight line distance between the posterior edge (base) of the merus and the tip of the extended dactyl when the merus propodus angle is 135° and the propodus-dactyl angle is 90° , which seems a reasonable approximation of maximum raptorial extension in prey capture. Over individuals of all sizes, the reach of *H. harpax* is clearly greater; the points for *H. harpax* overlap those of none of the other species, while these four species extensively overlap each other. Paired comparisons of *H. harpax* with each of the other four species yielded *t* values of 11.47

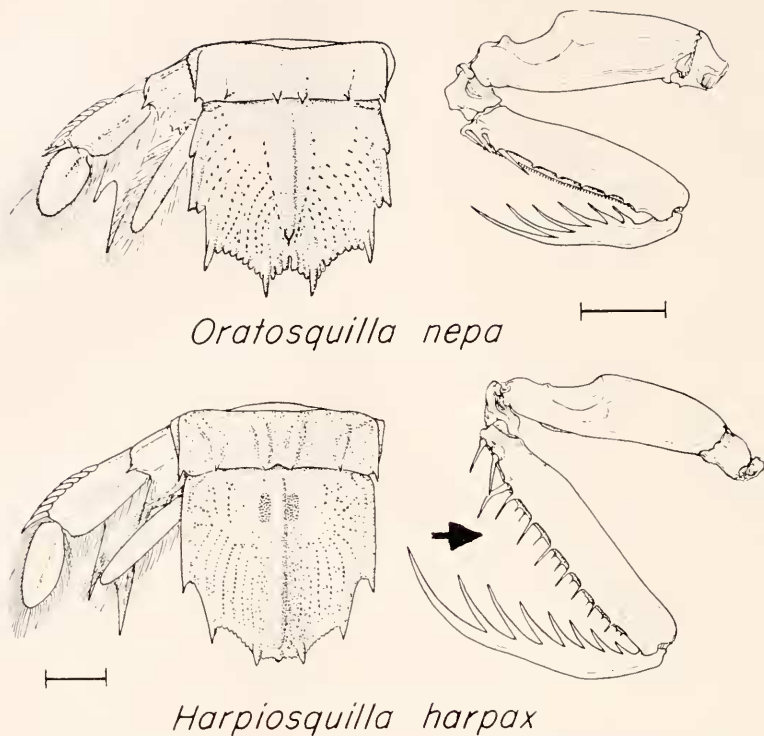


FIGURE 1. Telsons and raptorial appendages (second maxillipeds) of two spearers. Arrow indicates propodal spines of the fish eating *H. harpax*. Scale lines are 1 cm. Other species of *Oratosquilla* and *C. scorpio* closely resemble *O. nepa*.

to 18.47 which were all significant at $P < 0.001$. It seems likely that the elongated, spined, and toothed raptorial apparatus of *H. harpax* is an adaptation for capturing fish.

The raptorial appendages of *C. scorpio* and *Oratosquilla* spp. apparently differ little from each other. The various segments in all these species are of approximately the same relative length as indicated, for example, in the measurements of reach plotted in Figure 3. The similarities are also apparent in Figure 2. There are only two apparent differences. First, there are five dactylar teeth in *C. scorpio* and six in *Oratosquilla*, but this character varies between five and six both within and between species of both genera (Manning, 1969a, 1971; Tirmizi and Manning, 1968). Secondly, *C. scorpio* has a slightly heavier appendage. The mean ratio of merus width to merus length, for example, was 0.39 in *C. scorpio* (range 0.37 to 0.42, $N = 27$) and 0.33 to 0.34 in the *Oratosquillas* (range 0.31 to 0.35; $N = 6$ for *O. woodmasoni*; $N = 28$ for *O. nepa*, and $N = 29$ for *O. inornata*); *C. scorpio* was significantly different from each *Oratosquilla* at $P < 0.001$ for the Median test (Siegel, 1956). The structure of the raptorial appendages suggests that, like *O. nepa* discussed above, if any of these species were able to capture fish, they would have difficulty holding and eating them.

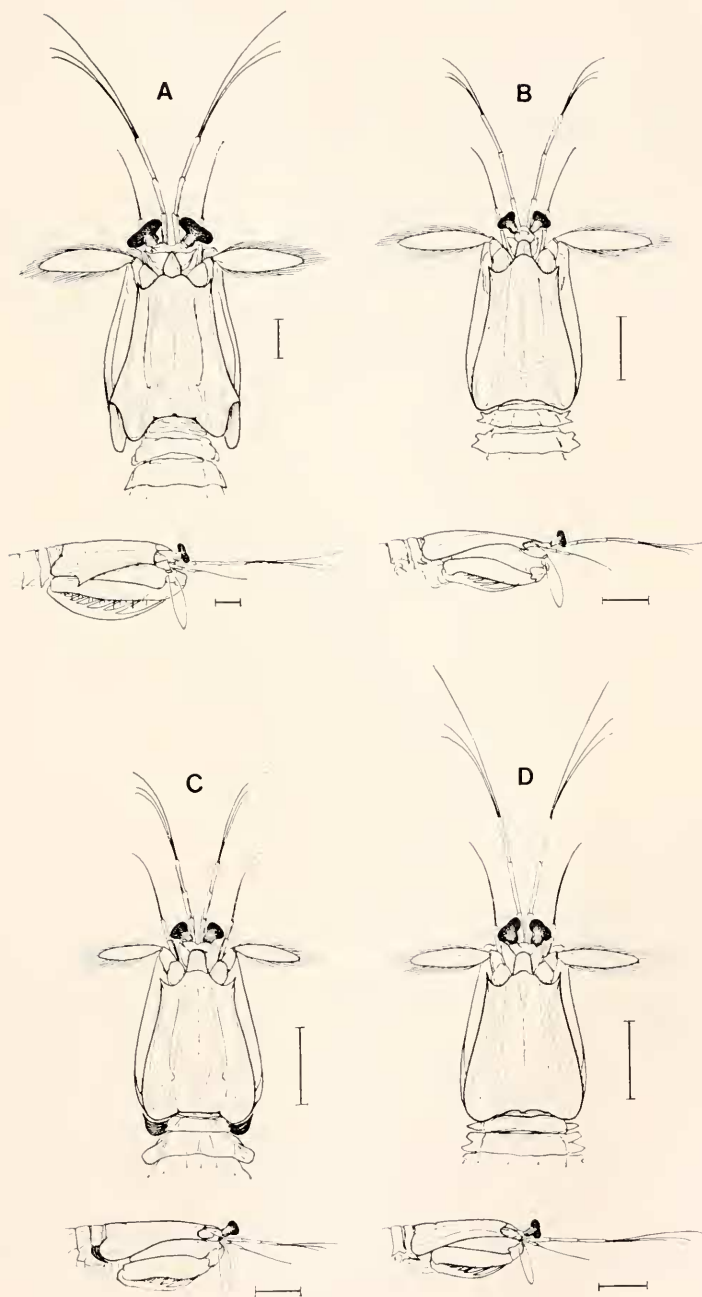


FIGURE 2. Relative proportions of cephalo-thoracic region of: A, *H. harpax*; B, *O. nepa*; C, *C. scorio*; and D, *O. inornata*. Scale lines are 1 cm. Note differences in size of eyes and length of antennules and elongated raptorial appendage of *H. harpax*. Eyes and antennules of *O. woodmasoni* have proportions similar to those of *O. inornata*.

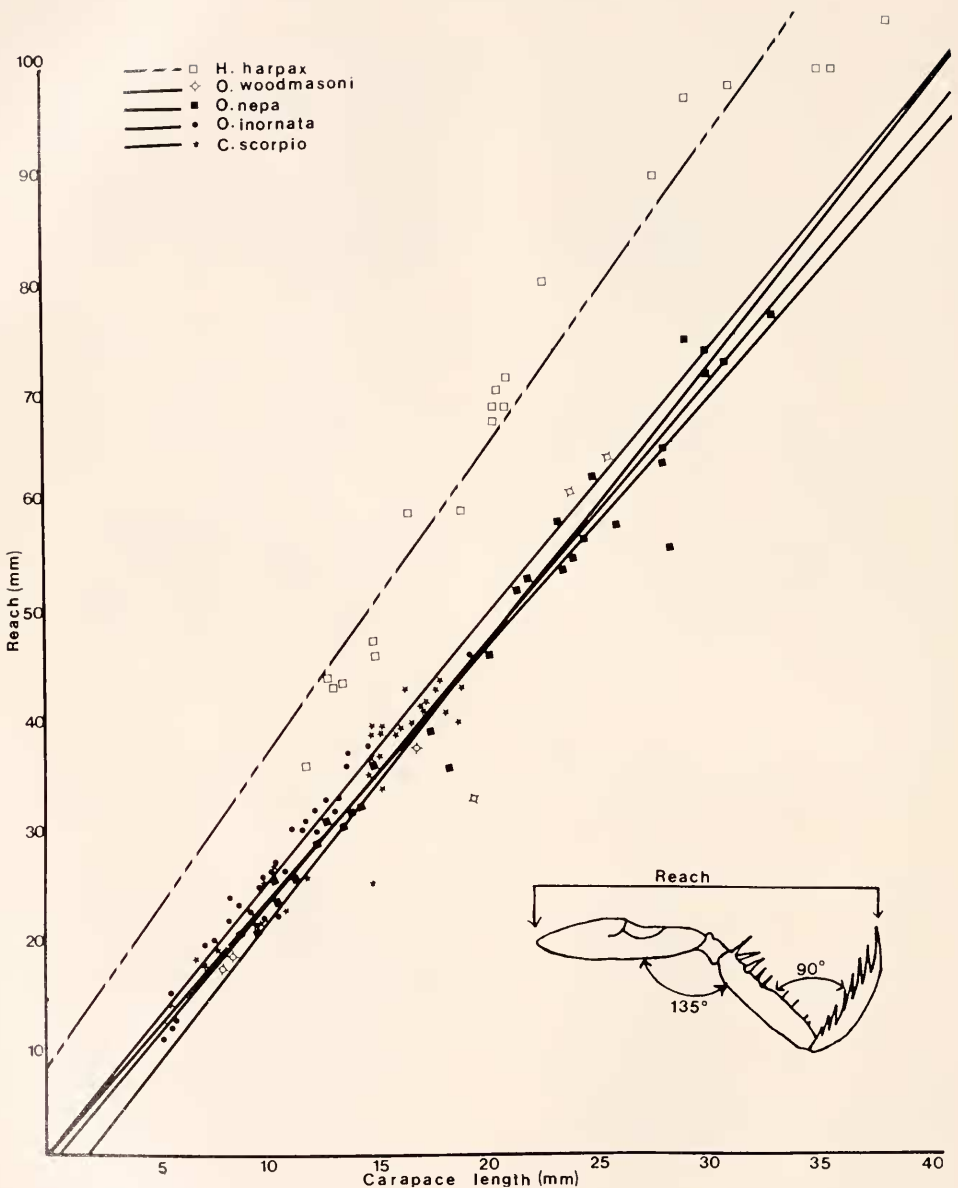


FIGURE 3. Reach (ordinate) as a function of carapace length (an indicator of body length) in five spearing stomatopods. Lines are least squares linear regressions. Note separation of *H. harpax* (a fish eater) and similarity of the other species.

The most important morphological differences among *C. scorpio* and the *Oratosquillas* with respect to prey capture may lie not in the raptorial appendages but rather in body size and the visual and chemoreceptors. These differences are

shown in Table 1 and Figure 2. (*O. woodmasoni* is included for qualitative comparisons only, since the specimens were from a different source.) It is clear that there is, first, a division by body size into a pair of small, *C. scorpio* and *O. inornata*, and a pair of large, *O. nepa* and *O. woodmasoni*, species based on maximum recorded carapace lengths. Differences in body proportions differed little between any of the species, including *H. harpax*, as indicated by abdominal width (at the eighth abdominal segment) to carapace length ratios (range 0.95 to 1.03 over all species) or carapace width to carapace length ratios (range 0.72 to 0.78). Significant differences between species, however, do occur in eyes and antennules (bearing the primary chemical receptors), with each pair of equivalent body size having a large-eyed long-antennuled species and a small-eyed short-antennuled species (*O. woodmasoni* is large-eyed). The ranges of the ratios of cornea width to eyestalk length for the large-eyed species did not overlap those of the small-eyed, nor did the small-eyed species overlap each other ($P < 0.001$ for any paired comparison using the Median test). Similarly, the ratios of antennule length to carapace length of the long-antennuled species did not overlap those of the short-antennuled, and the latter again failed to overlap each other ($P < 0.001$, Median tests). The fish predator, *H. harpax*, has both long antennules and the largest eyes. Such differences as occur in prey taken may thus depend in part on differences in sensory structures used to detect and stalk prey.

To summarize, the fish predator *H. harpax* differs from *C. scorpio* and the *Oratosquilla* species in having a relatively longer raptorial appendage and a larger eye. These latter species differ very little in the morphology of the raptorial appendage but do differ markedly in body size or in the relative sizes of eyes and antennules.

Burrows and burrowing behavior

Burrows of all the stomatopods discussed in this paper except *Harpiosquilla harpax* were observed in the field. Of the four species whose burrows were found, *Cloridopsis scorpio* digs the most complex structure. The entrance to the burrow is a circular opening frequently covered, except for a small central opening, with a thin sheet constructed of mud, mixed with a secretion produced by the animal presumably from glands in the mouth region. The entrance leads into a smooth tube, lined with mud mixed with secretion, proceeding vertically downward for approximately 5–15 cm depending on the size of the animal. The tube then bends and proceeds horizontally and somewhat circuitously to the bottom of the entrance tube of the second entrance; the walls of this portion of the burrow were not particularly smooth and, in appropriate substrates, were lined with broken shell. Roughly one-fourth of the observed burrows possessed a third entrance so that the burrow was more or less Y-shaped, and a few had an ovoid side chamber. The diameter of the burrow tube along its entire length was only slightly larger than the diameter of the occupying stomatopod, and total length of the burrow, as measured by inter-entrance distance on the surface, was directly proportional to the size of the occupant (Dingle and Caldwell, 1975). *C. scorpio* burrows were longer than those of correspondingly sized *Oratosquilla inornata* and *O. nepa*, even without consideration of the twists and turns (Dingle and Caldwell, 1975).

The burrows of the three species of *Oratosquilla* were quite similar. Again the entrance hole was frequently covered with a cap of material made of mud and secretions produced by the animal. Beyond the entrance a smooth-walled tube, lined with mud and secretion and roughly the diameter of the animal, extended vertically downward for a few centimeters before turning 90° and proceeding horizontally to the vertical tube leading to the second entrance. In contrast to *C. scorpio* burrows, the horizontal tube was lined with smooth walls, did not twist and turn, and was greater in diameter than the occupying stomatopod. In *O. inornata* the diameter of the tube was approximately five times the diameter of the animal while in *O. nepa* and *O. woodmasoni*, it was roughly three times the diameter. Again, burrow length was proportional to length of the animal.

Laboratory observations of burrow construction by *C. scorpio* and *O. inornata* reveal that the process is similar in the two species. *C. scorpio* begins by drawing up mud with the maxillipeds, pushing it back beneath the abdomen, and then fanning with the pleopods to push the material out behind into a small mound. After a few minutes the animal is lying in a trench. It then digs forward and downward until it gathers a load of mud, and then deposits this material in the trench after turning around. At first this material removed from the incipient burrow is tamped down in the trench, but as the trench fills and the burrow lengthens, some of it is apparently mixed with secretions and pasted against the sides of the nascent entry tube. In about ten minutes the entry tube is 3–4 cm deep, and the animal then starts to dig at about a 60° angle gradually leveling off to dig horizontally. Mud is scooped up into a basket formed by the maxillipeds, the stomatopod then somersaults, and finally it brings the load to the entrance and deposits it by coming roughly half a body length out of the burrow. Any caving in of the walls is repaired immediately by plastering mud mixed with secretion over the site of the cave in. Burrows in the laboratory took 12 hours to complete, but excessive caving in as a result of loosely packed mud may have extended the time beyond that normally required in natural substrates.

O. inornata differed somewhat from *C. scorpio* in the initial stages of burrow construction in that it did not form a trench. An entry was begun by reaching directly downward with the maxillipeds, bringing up a load of mud, and dispersing it by fanning much like *C. scorpio* but less vigorously. When the tube is 3–4 cm deep, the animal dives in for the first time to obtain a load and then somersaults to bring it to the surface. From here the process duplicates that of *C. scorpio* except that the initial turn in the tube is an abrupt 90° rather than the more gradual 60° turn of *C. scorpio*. In both species, once a burrow is completed (by turning upward until the surface is reached) a cap is constructed over each entrance with a small hole in the middle often virtually invisible. The animals then spend most of their time at one entrance with only eyes and antennules projecting from the burrow and with antennules kept flat on the substrate surface.

Agonistic behavior

The behavioral acts observed in ten minute, open arena encounters between two size and sex matched stomatopods are indicated in Table II for the three species for which such data were collected. Briefly, these acts can be described as follows:

TABLE II

Number of acts of various types performed by three squillid species in unisexual paired ten minute encounters in an open arena.

Species	Acts							Antennular contact	Total	N	Mean**
	Approach	Head-up	Lunge	Strike	Chase	Avoid	Follow				
<i>C. scorpio</i> ♂ (I)*	9	2	9	7	2	5		17	51	6	8.5
<i>C. scorpio</i> ♂ (F)	1		8	1	3	37		6	56	6	9.3
<i>C. scorpio</i> ♀ (I)	7	3	2	6		9		22	49	7	7.0
<i>C. scorpio</i> ♀ (F)		1		1	7	34	1	5	49	7	7.0
<i>O. inornata</i> ♂ (I)	10		2	5		14		39	70	10	7.0
<i>O. inornata</i> ♂ (F)	2		3	2	6	83	6	11	113	10	11.3
<i>O. inornata</i> ♀ (I)	25		3	8		24	9	70	139	11	12.7
<i>O. inornata</i> ♀ (F)	3		3	5	3	126	16	13	169	11	15.4
<i>O. nepa</i> ♂ (I)	17			5		6		21	49	9	5.5
<i>O. nepa</i> ♂ (F)			1	3		27	3	29	63	9	7.0
<i>O. nepa</i> ♀ (I)	33		1	4		2	1	57	98	10	9.8
<i>O. nepa</i> ♀ (F)			1	4		68	2	52	127	10	12.7

* I = initial acts; F = following acts (see text).

** Mean = total column divided by N column (where N = number of interacting pairs) and indicates mean number of acts per 10 min interaction per interacting pair.

approach, a direct, deliberate advance toward another animal with eyes and antennules pointing forward; *head-up*, the cephalo-thorax is raised and eyes and antennules are directed forward; *lunge*, a short rapid forward movement directed to another animal; *strike*, a blow delivered to another individual by the closed dactyls; *chase*, rapid pursuit of another animal; *avoid*, rapid and abrupt swimming or turning away; *follow*, an unburied directed movement toward an animal which is moving away; and *antennular contact*, antennular palpation of the body or "fencing" with the antennules of another animal. More detailed descriptions of most of these acts are given in Caldwell and Dingle (1975).

The data in Table II are compiled from matrices of inter-individual, two-act sequences of initial and following acts assembled for each species (several such matrices are presented in Dingle, 1969). Briefly, these matrices listed the acts which occurred as initial acts by one animal in such two-act sequences, and then indicated the number of times a specified act by the second animal followed a given initial act. The row totals thus gave the number of times each act initiated a sequence and the column totals indicated the frequency of occurrence as following acts. These totals were then arranged as the data in Table II; for each sex of each species, the number of times each act occurred as an initial and as a following act is presented. [Note that if an act was not followed by a response from the other animal, it is not included in the table. Therefore, the data here, especially those on strikes, do not exactly match those reported in Dingle and Caldwell (1975) and Caldwell and Dingle (1975) which include all acts.] Since the species discussed here spent only a small proportion of their encounter time interacting, and

since their behavior consisted predominantly of the acts avoid and antennular contact, the full interaction matrices are omitted.

The predominance of these two acts, indicates that there was little agonistic behavior in open arena encounters of these three species. Antennular contact is a general response to encountering any object in the environment. It was rarely followed by an overtly aggressive response, such as a lunge or a strike, and was usually broken off when one or both animals involved avoided. Further, the most frequent response to a contact between two animals was avoidance by one and often by both. Again, response to this by the overtly aggressive act, chase, was rare in *C. scorpio* and *O. inornata* and absent altogether in *O. nepa*. If a strike, the most aggressive act, did occur, it was most frequently as an initial act in *C. scorpio* and *O. inornata*; in *C. scorpio*, strikes were almost never reciprocated with a following aggressive act and in *O. inornata* infrequently so. Strikes occurred with about equal frequency as initial and following acts in *O. nepa* but were uncommon in either case. The only possibly aggressive act which was common was approach. In these species, however, unlike the smashing gonodactylids (Dingle and Caldwell, 1969; Caldwell and Dingle, 1975), the approach is not an overtly aggressive act. Rather, it is leisurely and in no obvious way different from a directed approach to any object, aside from a potential food item, that might attract a stomatopod's attention. Similarly, following is indistinguishable from movement toward any object slowly moving away.

Thus, only three acts can clearly and unambiguously be considered agonistic: lunge, strike, and chase. Their infrequency attests to the generally peaceful behavior of the animals in these encounters. Based on the evidence available, *C. scorpio* seems to be the most aggressive species as judged by the greater proportion of these agonistic acts (Table II). The sum of all lunges, strikes, and chases in *C. scorpio* interactions was 46 acts representing 22.4% of the total of 205 acts (total column, summed) in this species. In contrast the 40 agonistic acts of *O. inornata* represent only 8.2% of the total and the 19 agonistic acts of *O. nepa* only 5.6% of the total for those species. The greatest proportion of avoids was shown by *O. inornata*, the species which overlaps *C. scorpio* most extensively in habitat (Dingle and Caldwell, 1975). Males of *C. scorpio* displayed agonistic acts more frequently than females, but there were no apparent sex differences in either of the *Oratosquillas*. Finally, head-up, a possibly agonistic act, occurred only in *C. scorpio* but did not occur with sufficient frequency to make any assessment of its role relative to agonism.

Burrow defense

Highly agonistic behavior was observed in both intra- and interspecific burrow defense interactions between individuals of *C. scorpio* and *O. inornata*. In a typical encounter an intruder, once it saw a burrow entrance, would immediately dive into the burrow, whereupon it was struck by the burrow occupant, resulting in its rapid retreat. Further attempts to enter the burrow were met in a similar manner. In both species the burrow defender occasionally came all the way out into the water column to strike. In general, *C. scorpio* was more persistent in attempting to enter burrows. This is reflected in the number of strikes delivered by the burrow occu-

pant in the five minutes beginning with the initial attempt at entry; in six *C. scorpio* intraspecific interactions, the mean was 4.5 ± 2.4 strikes, while in seven *O. inornata* intraspecific interactions the mean was 2.14 ± 2.95 strikes. Also, in two of the *C. scorpio* cases and one *O. inornata* case an intruder gained entry, and there followed grasping with the maxillipeds and striking within the burrow itself. The act, grasp, can thus be added to the list of overtly aggressive acts in these species, although it should be noted that it occurred in burrow defense only and not in open arenas. One eviction of the burrow occupant by the intruder occurred in the six *C. scorpio* interactions, and two evictions occurred in the seven *O. inornata* interactions. Dives into the burrow, strikes, and grasps were all clearly agonistic acts.

The generally more aggressive behavior of *C. scorpio* was also demonstrated in interspecific burrow defense interactions (Dingle and Caldwell, 1975). In all eight trials in which *C. scorpio* defended against *O. inornata*, it successfully defended. In the reverse situation, *O. inornata* was evicted by *C. scorpio* in eight of eleven trials. Based on both burrow defense and open arena interactions, it can be concluded that *C. scorpio* is the most aggressive of the species studied.

DISCUSSION

H. harpax differs from the other squillids in the overall length of the raptorial appendage, in the size of the eye, and in hunting methods. The length difference, obvious in Figure 3, clearly differentiates *H. harpax* from the other species studied, all of which were similar to each other. The greater reach and larger eye are presumably advantageous in the capture of more elusive and alert prey such as fish, for tests in the laboratory indicate that *H. harpax* is a capable fish predator.

The three *Oratosquilla* species and *Cloridopsis scorpio* all apparently feed largely on arthropods, thin-shelled pelecypods, and annelids. The similarity in raptorial appendages is striking and suggests that the evolution of the raptorial apparatus has been conservative in these genera. An example of the similarity is shown by the plot for reach (Fig. 3); dactylar tooth number is also similar. It would thus seem that resource partitioning between these species would not be on the basis of the reach or number of dactylar teeth of the trophic apparatus. This conclusion is given further support by the results of Holling, Dunbrack, and Dill (1976). They find that optimal prey size calculated from the mechanics of the trophic apparatus plotted against the cube root of body size increases linearly in a plot that includes two species of praying mantis and two stomatopods, *Pseudosquilla ciliata* and *Oratosquilla oratoria*. There is probably some partitioning on the basis of relative thickness of prey armor, since the more massive raptorial appendage of *C. scorpio* should endow this species with a more powerful strike.

In view of the qualitatively similar food items apparently taken by the *Oratosquilla* and *C. scorpio* and the marked similarity in raptorial appendages across the four species, three possible mechanisms for resource partitioning are suggested by the data. First, major differences among the species do occur in body size with two large and two small species (Table I). Interestingly, these stomatopods do not sort out with one large and one small species per habitat as is often reported (*e.g.*, for aquatic insects, Hutchinson, 1959; Streams and Newfield, 1972). Rather, habitat sorting occurs because the small species predominate inshore where the two

large species are rare (Dingle and Caldwell, 1975), and the large predominate offshore where they are regularly caught by fishermen. (Other small crustaceans were taken by the fishermen, so the small stomatopods were not simply escaping the nets.) Secondly, other observations suggest some habitat separation within each set of species. *O. inornata* on the Ang Sila mudflat tended to be more associated with rock outcrops than was *C. scorpio* (Dingle and Caldwell, 1975) and tended to occur alone, although it was relatively uncommon, on mudflats associated with mangroves. *O. woodmasoni* was far less tolerant of temperature and oxygen stress than was *O. nepa*, suggesting that it occurs on substrates less subject to fluctuations in these factors.

Thirdly, the most conspicuous differences between species within the large and small size classes of stomatopod are in the sensory structures (Table I). Although the optics of the arthropod eye are complex (*e.g.*, Horridge, 1977), larger eyes generally lead to increased visual acuity, and the fish predator *H. harpax*, indeed, has the largest eyes. The large-eyed *Oratosquillas* probably have increased visual acuity relative to the small-eyed species and increased capability of capturing more distant or more rapidly moving prey. In Crustacea, including stomatopods, the antennules are the primary appendages for chemoreception, and there is integration of inputs from these in the eyestalk ganglia (Maynard and Dingle, 1963; Maynard and Yager, 1968; Hazlett, 1971a, b). There is close coordination between these two sensory systems in prey capture, and differences could promote resource partitioning on the basis of prey type. Within body size classes and hence within habitats, differences in sensory capability could form the basis for resource partitioning as a function of prey items taken.

Differences in body proportions and in trophic apparatus have been one main focus of attention among ecologists attempting to assess resource partitioning. Indeed treatment of data with respect of these morphological variables has often reached a high level of sophistication especially with respect to birds (Schoener, 1965; Karr and James, 1975). Sensory structures have received far less attention, although differences in capability are implicit in many ecological generalizations concerning partitioning (Schoener, 1974). Our data from stomatopods suggest that greater attention to sensory differences with respect to foraging strategies may prove rewarding, especially in those cases where differences in trophic apparatus are minimal or absent.

Agonistic behavior in stomatopods has clearly co-evolved with the structure of the raptorial appendage (Caldwell and Dingle, 1975). In contrast to the species discussed here, most Gonodactylidae have a heavy hammer-like dactyl evolved for smashing hard or armored prey and generally show vigorous agonistic interaction. Only lunge, strike, chase, and in burrow defense, grasp, are unambiguously agonistic acts in these squillids. None appears to have especially evolved for agonism since all are used in prey capture; there are, in other words, no ritualized acts (Hazlett, 1972a). In contrast, the smashing gonodactylids show a highly elaborated meral display functioning agonistically as a threat, a characteristic coil used as a defense posture, and in general possess a more extensive agonistic repertoire (Dingle and Caldwell, 1969; Caldwell and Dingle, 1975).

The frequency with which agonistic acts occur also differs between these

squillids and gonodactylids. The maximum mean number of acts per interacting pair in open arenas in the squillids is 15.4 per ten minute interaction for female *O. inornata* (Table II). This is less than the mean for all but one of the gonodactylids so far analyzed (Caldwell and Dingle, 1975). In the latter group of species the mean ranged from 9.4 in the least active *Gonodactylus platysoma* to 42.6 in the highly active *G. zacae*. For most of the categories in Table II, the mean is below 9.4 suggesting that these squillids are generally less active than even the most sluggish of the gonodactylids. The difference between the two families is still more conspicuous when individual acts are considered. The clearly agonistic act, strike, for example, makes up a very small proportion of acts in Table II (maximum 13.7% of the initial acts of male *C. scorpio*). In contrast, the initial acts of two typical gonodactylids, *G. bredini* and *G. spinulosus*, consist of 25.5 and 19.0% strikes, respectively (Dingle, 1968, 1972).

Two factors, prey choice and shelter availability, seem to be the major selective forces molding stomatopod agonistic behavior (Caldwell and Dingle, 1975). The closed dactyl of spearers, when used in striking, inflicts relatively less damage on another animal than the hammer-like dactyl of smashers. The squillids also live on mud bottoms and are capable of constructing their own burrows; they are thus not shelter limited. As a consequence, neither prey choice nor competition for shelter would seem to impose strong selection for well-developed agonistic behavior. However, within the group, *C. scorpio*, with the greatest investment in burrow construction and the heaviest raptorial appendage, is the most agonistic.

In the gonodactylids, the raptorial appendage has evolved to smash armored prey and has thus become an effective aggressive weapon. These species occupy pre-existing cavities in hard substrates and are apparently shelter limited. Agonistic behavior and co-evolved body armor, especially involving the telson used in the defensive coil, are therefore conspicuous features of these species. Within the group, the least shelter-limited species, *G. platysoma*, is also the least agonistic. Both within and between family comparisons suggest shelter availability as a selective agent (Caldwell and Dingle, 1975).

Parallels to the evolution of agonistic behavior in stomatopods occur in decapods. Striking and grasping are conspicuous parts of the agonistic repertoire of many species possessing a large crushing cheliped, as in crayfish (e.g., Bovbjerg, 1956; Stein, 1976); whereas they are less obvious or absent when chelipeds are small as in majid crabs (Schöne, 1968; Hazlett, 1972b). Shelter-limited species such as xanthid crabs (Preston, 1973; Hazlett, 1976) and snapping shrimp (Alpheidae) (Schein, 1975) are also markedly aggressive. But in spite of these similarities, stomatopods appear to be far more conservative in the evolution of behavior and morphology. The greatest elaborations are the modifications of raptorial appendages and of telson armor in the gonodactylids accompanied by behaviors such as the meral spread and coil postures (Caldwell and Dingle, 1975, 1976). In contrast, decapod species have frequently evolved elaborate structural changes in the cheliped for use in agonistic and sexual behavior, with the snapping shrimps and fiddler crabs (*Uca*) (Crane, 1966) being outstanding examples. This paper has analyzed some of the consequences of evolutionary conservatism in the squillids; the gonodactylids will be treated in detail in future publications.

Prof. T. Piyakarnchana arranged for us to use the station at Ang Sila and, in

general, smoothed our way in Thailand. Mr. S. Tameyavanish helped us locate animals and provided logistical support; Mr. P. Naiyanetr and Dr. R. B. Manning identified the species. Dr. M. Reaka and Ms. J. Dingle provided field assistance. The figures were prepared by Ms. E. Reid and J. Dingle, and the manuscript was read by Drs. R. V. Bovbjerg, F. C. James, and R. B. Manning. Supported by U. S. National Science Foundation Grants GB-37046-7 and BNS 74-22717-8.

SUMMARY

Agonistic and feeding behavior and morphological structure were studied in five stomatopod crustaceans with raptorial appendages adapted for spearing prey. Agonistic behavior was less frequent and less vigorous than in species adapted for smashing. Of the spearers, the most aggressive species, *Cloridopsis scorpio*, possessed a heavier raptorial apparatus and constructed the most complex burrow. *Harpisquilla harpar* preyed on fish and had the longest raptorial appendages and largest eyes. The remaining species (three *Oratosquilla* spp. and *C. scorpio*) possessed similar raptorial appendages but sorted out by water depth, body size, eye size, and length of antennules. The latter two measurements suggest that differences in the structure and function of sensory systems may be important considerations in the analysis of foraging strategies and resource partitioning.

LITERATURE CITED

- BOVBJERG, R. V., 1956. Some factors affecting aggressive behavior in crayfish. *Physiol. Zool.*, **29**: 127-136.
- CALDWELL, R. L., AND H. DINGLE, 1975. Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften*, **62**: 214-222.
- CALDWELL, R. L., AND H. DINGLE, 1976. Stomatopods. *Sci. Am.*, **234**(1): 80-89.
- CALDWELL, R. L., AND H. DINGLE, 1977. Variation in agonistic behavior between populations of the stomatopod, *Haptosquilla glyptocercus*. *Evolution*, **31**: 220-223.
- CRANE, J., 1966. Combat, display and ritualization in fiddler crabs (Ocypodidae, genus *Uca*). *Philos. Trans. R. Soc. Lond. Biol. Sci.*, **251**: 459-472.
- DINGLE, H., 1969. A statistical and information analysis of aggressive communication in the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). *Anim. Behav.*, **17**: 567-581.
- DINGLE, H., 1972. Aggressive behavior in stomatopods and the use of information theory in the analysis of animal communication. Pages 126-156 in H. A. Winn and B. Olla, Eds., *Behavior of marine animals. Current perspectives in research, Vol. I: Invertebrates*. Plenum Press, New York.
- DINGLE, H., AND R. L. CALDWELL, 1969. The aggressive and territorial behavior of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). *Behavior*, **33**: 115-136.
- DINGLE, H., AND R. L. CALDWELL, 1975. Distribution, abundance, and interspecific agonistic behavior of two mudflat stomatopods. *Oecologia*, **20**: 167-178.
- HAZLETT, B. A., 1971a. Non-visual functions of crustacean eyestalk ganglia. *Z. Vergl. Physiol.*, **71**: 1-13.
- HAZLETT, B. A., 1971b. Chemical and chemotactic stimulation of feeding behavior in the hermit crab *Petrochirus diogenes*. *Comp. Biochem. Physiol.*, **39A**: 665-670.
- HAZLETT, B. A., 1972a. Ritualization in marine Crustacea. Pages 97-125 in H. A. Winn and B. Olla, Eds., *Behavior of marine animals. Current perspectives in research, Vol. I: Invertebrates*. Plenum Press, New York.
- HAZLETT, B. A., 1972b. Responses to agonistic postures by the spider crab *Microphrys bicornutus*. *Mar. Behav. Physiol.*, **1**: 85-92.

- HAZLETT, B. A., 1976. Agonistic behavior of two sympatric species of xanthid crabs, *Leptodius floridanus* and *Hexapanopus angustifrons*. *Mar. Behav. Physiol.*, **4**: 107-119.
- HOLLING, C. S., R. L. DUNBRACK, AND T. M. DILL, 1976. Predator size and prey size: presumed relationship in the mantid *Hierodula coarctata* Saussure. *Can. J. Zool.*, **54**: 1760-1764.
- HORRIDGE, G. A., 1977. The compound eye of insects. *Sci. Am.*, **237**(1): 108-120.
- HUTCHINSON, G. E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.*, **93**: 145-159.
- KARR, J. R., AND F. C. JAMES, 1975. Ecomorphological configurations and convergent evolution. Pages 258-291 in M. L. Cody and J. M. Diamond, Eds., *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts.
- MANNING, R. B., 1969a. A review of the genus *Harpiosquilla* (Crustacea, Stomatopoda) with descriptions of three new species. *Smithson. Contrib. Zool.*, **36**: 1-41.
- MANNING, R. B., 1969b. *Stomatopod Crustacea of the Western Atlantic*. University of Miami Press, Coral Gables, Florida.
- MANNING, R. B., 1971. Keys to the species of *Oratosquilla* (Crustacea: Stomatopoda) with descriptions of two new species. *Smithson. Contrib. Zool.*, **71**: 1-16.
- MAYNARD, D. M., AND H. DINGLE, 1963. An effect of eyestalk ablation on antennular function in the spiny lobster, *Panulirus argus*. *Z. Vergl. Physiol.*, **46**: 515-540.
- MAYNARD, D. M., AND J. G. YAGER, 1968. Function of an eyestalk ganglion, the *medulla terminalis*, in olfactory integration in the lobster, *Panulirus argus*. *Z. Vergl. Physiol.*, **59**: 241-249.
- PRESTON, E. M., 1973. A computer simulation of competition among five sympatric congeneric species of xanthid crabs. *Ecology*, **54**: 469-483.
- SCHEIN, H., 1975. Aspects of the aggressive and sexual behavior of *Alpheus heterochaelis* Say. *Mar. Behav. Physiol.*, **3**: 83-96.
- SCHOENER, T. W., 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution*, **19**: 189-213.
- SCHOENER, T. W., 1974. Resource partitioning in ecological communities. *Science*, **185**: 27-39.
- SCHÖNE, H., 1968. Agonistic and sexual display in aquatic and semiterrestrial brachyuran crabs. *Am. Zool.*, **8**: 641-654.
- SIEGEL, S., 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York.
- STEIN, R. A., 1976. Sexual dimorphism in crayfish chelae: functional significance linked to reproductive activities. *Can. J. Zool.*, **54**: 220-227.
- STREAMS, F. A., AND S. NEWFIELD, 1972. Spatial and temporal overlap among breeding populations of New England *Notonecta*. *Univ. Conn. Occas. Pap. Biol. Sci. Ser.*, **2**: 139-157.
- TIRMIZI, N. M., AND R. B. MANNING, 1968. Stomatopod Crustacea from West Pakistan. *Proc. U. S. Nat. Mus.*, **125**: 1-48.